LIGNIFICATION OF MATURE PHLOEM IN HERBACEOUS TYPES

Carl L. Wilson

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Secondary growth in the woody stems of gymnosperms and angiosperms often results in the formation of annual rings in the xylem, but in the phloem no similar arrangement of elements is usually to be observed. The sieve tubes, which are generally the principal elements of the phloem, are crushed at the end of each period of growth by the pressure of surrounding cells and tissues. To these changes taking place in the secondary phloem the term *obliteration* has been applied for a long time. The alterations are initiated by the disappearance of the contents of the sieve tubes at the end of each growth period, soon followed by a crushing and distortion of the sieve tubes, and, in the case of angiosperms, of companion cells also. The sieve plates may be broken down, and the wall of the sieve tube takes on a swollen appearance. In an advanced condition of obliteration, the lumen of the sieve tube entirely disappears, being represented only by a line, and the whole mass of crushed sieve tubes takes on a horn-like consistency. During these changes the structure of the phloem parenchyma does not appear to be affected.

The term horn prosenchym (*Horngewebe*) was applied by Wigand (1863) to such a mass of crushed tissue. The principal facts concerning the transformations undergone by the phloem of woody angiosperms have been generally known since the time of this writer. Previous to this date both Oudemans (1862) and Rauwenhoff (1869) appear to have described obliterated structures in the phloem, Oudemans in 1855, and Rauwenhoff in 1859. These two writers, together with Moeller (1875) and Tschirch (1889), showed the crushed tissue to be composed of obliterated sieve tubes. Tschirch pointed out that the sieve tubes, including cambiform cells and companion cells, having lost the principal portion of their contents at the end of the growing season, become pressed together through the turgor of neighboring cells, so that only a small, cleft-shaped lumen remains. He believed that a subsequent thickening of the wall does not take place. De Bary (1884) indicated some doubt as to the extent to which the cambiform cells of the phloem are affected in obliteration, although he described the crushing of the sieve tubes. Bliesnick (1891) found that the phloem parenchyma takes no part in obliteration. His conclusions are essentially the same as those of Tschirch with regard to the causes of obliteration. Lignification of sieve plates was found in Clematis, and in another case he mentions that he found complete lignification of the obliterated phloem elements. His results differ from those of previous investigators in that

he found sieve tubes and companion cells crushed, but never phloem parenchyma.

Publications on the changes undergone by the phloem of herbaceous types are few. Schumann (1890), in his work on the anatomy of the composite stem, reports finding lignification of the sieve tubes and companion cells in two species of Compositæ, *Scorzonera Hispanica* and *Aster thyrsiflorus*, finding the sieve plates especially to be lignified. Boodle (1902), in his first note on the subject, reports finding lignification of the sieve tubes and companion cells in two plants of *Helianthus annuus;* lignification of contents, though not of the walls of sieve tubes, was obtained in the root. In repeating the work of Vesque and Boubier, Boodle found no lignification of sieve tubes in *Betula alba*, such as had been described by these workers. In a later publication, Boodle (1906) reported results of the examination of additional material of Helianthus, in the course of which examination he investigated eleven plants of *H. annuus*, one plant of *H. tuberosus* L., and the stems of *H. laetiflorus* Pers. and *H. decapetalus* L. The observations previously recorded were confirmed both for *H. annuus* and for the other species mentioned. His conclusions may be summed up as follows: the sieve tubes and companion cells in the stems of the species mentioned are normally lignified; the contents of the sieve tubes in the root become lignified, whereas lignification of phloem parenchyma is rare, having been observed in only one case.

The present investigation was undertaken to determine whether there exist any departures from the usual unlignified and uncrushed condition of the phloem in herbaceous types, without reference to certain alterations known to be brought about by diseased conditions, such as phloem necrosis in leafroll of potatoes.

In order to determine the occurrence of such unusual conditions, the mature stems of a large number of herbaceous plants were examined by means of free-hand sections.[1] No conditions departing from the usual were found, until species of the Compositae were examined. In a number of species of this family extensive lignification of the phloem was found to have taken place. This lignification would seem to include only the parenchyma of the phloem, other elements presenting the usual appearance of a phloem group of the herbaceous type. The lignified elements appear with greatly thickened walls, and, but for their position, would in most cases be difficult to distinguish from the tracheids of the xylem. In a phloem group in which such lignification is found, it is practically certain that all of the phloem parenchyma becomes lignified, with the exception of those elements most recently formed, found next to the cambium. The parenchyma cells of this region, upon reaching maturity, will of course

[1] The sections were stained on the slide with phloroglucin and concentrated hydrochloric acid, the lignified portions giving the characteristic reaction. Portions of stems showing typical lignification were then imbedded in celloidin, sectioned, and stained with haematoxylin and safranin.

also become lignified. No conditions such as were described by Schumann and Boodle have been noted. The sieve tubes and companion cells have not been found to be lignified, and appear normal and functional in every way. In the transverse section of a stem shown in figure 1, Plate XIII, (upper left), a phloem group is seen enclosed between the bundle cap and the xylem. All the elements exclusive of the sieve tubes and companion cells appear lignified with the exception of several groups just outside the cambium; these latter may be tissue which has not yet matured, or may consist of sieve tubes. In the transverse section shown in figure 2 (upper right), the whole of the phloem is not shown, but the same condition is seen to prvail. Some unlignified elements are seen just under the bundle cap; these are probably sieve tubes of the protophloem. Figure 3 (lower left) is an enlarged view of a portion of the same region shown in figure 2, showing unlignified sieve tubes and companion cells surrounded by lignified parenchyma. Figure 4 (lower right) represents a longitudinal section through a region similar to that shown in the preceding figure. The walls of the sieve tubes (*s*) appear black, in contrast to the lighter color of the lignified parenchyma walls. Several cambiform cells with lignified walls are indicated at *x*, a nucleus and stored food material being clearly shown.

Some correlation, at least, appears to exist between the presence of lignification in the stem and in the root. In an examination of the tap roots of several species possessing lignification, lignification of phloem parenchyma was found. The following plants were found to possess lignified phloem elements in both root and stem:

Solidago arguta Ait.	*Aster ericoides* L.
S. rugosa Mill.	*A. umbellatus* Mill.
S. serotina Ait.	*A. puniceus* L.

Solidago graminifolia (L.) Salisb.

As stated previously, no conditions comparable to those described by Boodle have been noted, either in *Helianthus annuus* or in other plants to which he referred. An examination of a large number of stems of *H. annuus* was made to find such conditions if possible. In one case only was a departure from the usual condition found. This was in a mature stem, about one half inch in diameter, which exhibited an unmistakable lignification of phloem parenchyma when examined by means of free-hand and microtome sections.

Referring to the following list, several interesting facts may be brought out. It will be noted that all the forms in which lignification has been found belong to the first series of the Compositae, the Tubuliflorae, no lignification having been found in any species falling within the Liguliflorae. Lignification does not seem to occur in all the species of a genus in which lignification has been found. Illustrations of this fact can be seen in nearly all the genera listed. It has also been found in a few cases, which could probably

be extended by further observation, that lignification is not found in every individual of the same species.

The following material has been studied in the course of the investigation:

SPECIES OF COMPOSITAE HAVING LIGNIFIED PHLOEM ELEMENTS

Grindelia squarrosa (Pursh) Dunal
Solidago latifolia L.
S. bicolor L.
S. puberula Nutt.
S. sempervirens L.
S. patula Muhl.
S. arguta Ait.
S. juncea Ait.
S. uniligulata (DC.) Porter
S. ulmifolia Muhl.
S. rugosa Mill.
S. nemoralis Ait.
S. canadensis L.
S. altissima L.
S. serotina Ait.
S. graminifolia (L.) Salisb.
Aster divaricatus L.
A. Schreberi Nees
A. macrophyllus L.
A. novae-angliae L.
A. patens Ait.
A. undulatus L.
A. cordifolius L.
A. Lowrieanus Porter
A. sagittifolius Wedemeyer
A. laevis L.
A. ericoides L. var. *villosus* T. & G.
A. multiflorus Ait.
Aster dumosus L.
A. vimineus Lam.
A. lateriflorus (L.) Britton
A. Tradescanti L.
A. paniculatus Lam.
A. junceus Ait.
A. prenanthoides Muhl.
A. puniceus L.
A. umbellatus Mill.
A. subulatus Michx.
A. angustus (Lindl.) T. & G.
Erigeron annuus (L.) Pers.
E. ramosus (Walt.) BSP.
E. canadensis L.
Sericocarpus asteroides (L.) BSP.
Anaphalis margaritacea (L.) B. & H.
Gnaphalium polycephalum Michx.
G. decurrens Ives
Helianthus annuus L.
Coreopsis tripteris L.
Achillea Ptarmica L.
A. Millefolium L.
Anthemis Cotula L.
Tanacetum vulgare L.
Artemisia caudata Michx.
A. Pontica L.
A. Absinthium L.

SPECIES OF COMPOSITAE EXAMINED AND FOUND TO CONTAIN NO LIGNIFIED PHLOEM ELEMENTS

Vernonia noveboracensis Willd.
V. altissima Nutt.
Eupatorium purpureum L.
E. hyssopifolium L.
E. sessilifolium L.
E. urticaefolium Reichard
Mikania scandens (L.) Willd.
Liatris scariosa Willd.
Solidago caesia L.
Erigeron pulchellus Michx.
Antennaria plantaginifolia (L.) Richards.
A. fallax Greene
A. neodioica Greene
A. petaloidea Fernald
Gnaphalium uliginosum L.
Inula Helenium L.
Polymnia canadensis L.
Silphium trifoliatum L.
Ambrosia trifida L.
A. artemisiifolia L.
Xanthium canadense Mill.
X. commune Britton
X. echinatum Murr.
Heliopsis helianthoides (L.) Sweet
Rudbeckia hirta L.
R. laciniata L.
Helianthus divaricatus L.
H. strumosus L.
H. decapetalus L.
H. tuberosus L.
Bidens discoidea (T. & G.) Britton
B. frondosa L.

Bidens vulgata Greene
B. comosa (Gray) Wiegand
B. cernua L.
B. Beckii Torr.
Galinsoga parviflora Cav.
Helenium autumnale L.
Anthemis tinctoria L.
Chrysanthemum Leucanthemum L. var. *pinnatifidum* Lecoq & Lamotte
C. Parthenium (L.) Bernh.
C. Balsamita L. var. *tanacetoides* Boiss.
Artemisia biennis Willd.
Tussilago Farfara L.
Erechtites hieracifolia (L.) Raf.
Senecio vulgaris L.
Cacalia atriplicifolia L.
Arctium Lappa L.
A. nemorosum Lejeune
Cirsium muticum Michx.
Cirsium pumilum (Nutt.) Spreng.
C. arvense (L.) Scop.
Centaurea Cyanus L.
C. nigra L.
Lapsana communis L.
Cichorium Intybus L.
Krigia virginica (L.) Willd.
Leontodon autumnalis L.
Tragopogon pratensis L.
Chondrilla juncea L.
Sonchus oleraceus L.
S. asper (L.) Hill
Lactuca scariola L.
Prenanthes serpentaria Pursh
P. trifoliolata (Cass.) Fernald
Hieracium aurantiacum L.
H. venosum L.
H. scabrum Michx.

SPECIES OF OTHER FAMILIES IN WHICH LIGNIFICATION HAS NOT BEEN FOUND

Saururus cernuus L.
Cannabis sativa L.
Rumex crispus L.
Polygonum Hydropiper L.
P. acre HBK.
P. virginianum L.
P. scandens L.
Atriplex patula L. var. *hastata* (L.) Gray
Amaranthus retroflexus L.
A. blitoides Wats.
Phytolacca decandra L.
Mollugo verticillata L.
Lychnis alba Mill.
Silene sp.
Saponaria officinalis L.
Ranunculus acris L.
Thalictrum dioicum L.
T. polygamum Muhl.
Anemone virginiana L.
Menispermum canadense L.
Sisymbrium officinale (L.) Scop.
Sedum purpureum Tausch
Potentilla monspeliensis L.
P. recta L.
Agrimonia gryposepala Wallr.
A. striata Michx.
Melilotus alba Desr.
Medicago sativa L.
Vicia villosa Roth
Lathyrus palustris L.
Amphicarpa monoica (L.) Ell.
Linum usitatissimum L.
Oxalis corniculata L.
Acalypha virginica L.
Althaea rosea Cav.
Lythrum Salicaria L.
Rhexia sp.
Oenothera biennis L.
Sanicula marilandica L.
Pastinaca sativa L.
Apocynum sp.
Asclepias incarnata L.
A. syriaca L.
Convolvulus sepium L.
Cuscuta Gronovii Willd.
Myosotis scorpioides L.
Verbena urticaefolia L.
Nepeta Cataria L.
Leonurus Cardiaca L.
Monarda didyma L.
Collinsonia canadensis L.
Solanum Dulcamara L.
Datura Tatula L.
Verbascum Blattaria L.
Linaria vulgaris Hill
Scrophularia leporella Bicknell
Plantago major L.
Dipsacus sylvestris Huds.
Cucurbita sativus L.
Echinocystis lobata (Michx.) T. & G.
Lobelia cardinalis L.
L. siphilitica L.

Summary

It has been commonly supposed that no crushing, or alterations involving a change in the chemical composition of the cell wall, occurs in the mature phloem of herbaceous angiosperms, although extensive alterations are known to take place in the mature woody stems of gymnosperms and angiosperms. It has been found, however, that within the series Tubuliflorae of the family Compositae, extensive lignification of the phloem parenchyma takes place in a number of species belonging to several different genera. These elements appear to retain their functional activity. The structure of the sieve tubes and companion cells is not affected.

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Department of Botany,
New York State College of Agriculture,
Cornell University

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EXPLANATION OF PLATE XIII

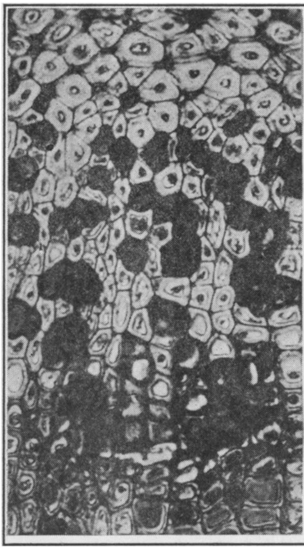
Fig. 1. Transverse section of phloem group from the stem of *Gnaphalium polycephalum*. Note contrast between lignified parenchyma and darkly stained, unlignified sieve tubes.

Fig. 2. Transverse section, stem of *Aster paniculatus*, showing portions of the bundle cap, protophloem, and secondary phloem.

Fig. 3. Enlarged view of a portion of the phloem group shown in figure 2.

Fig. 4. Longitudinal section of the phloem of the stem of *Aster novae-angliae*, showing unlignified sieve tubes (*s*) and lignified parenchyma (*x*).

1



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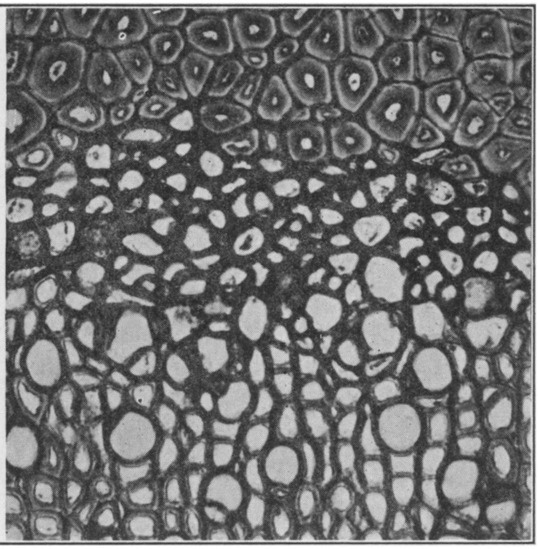

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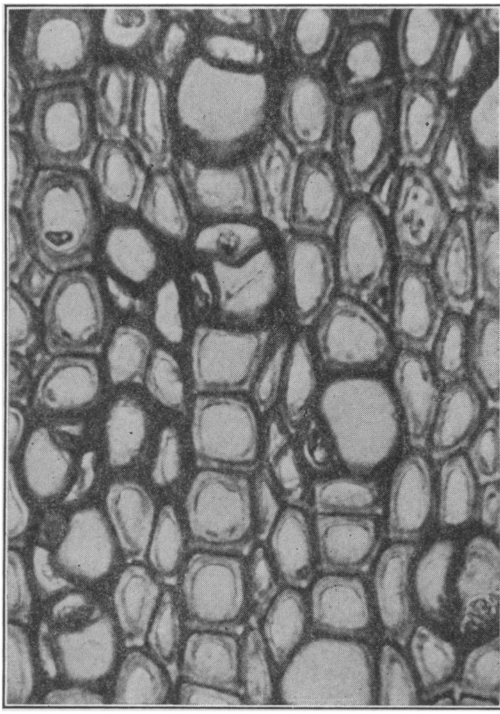

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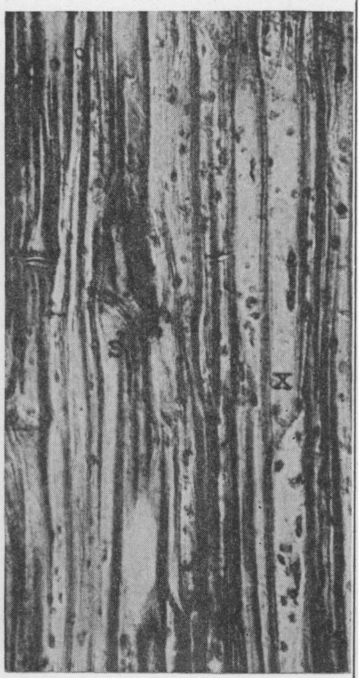

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